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Art. V.—*The Lignotubers of Eucalypt Seedlings.*

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(With Plates X., XI., and 7 Text Figures).

[Read 12th June, 1924].

During their early stages of growth the great majority of the Eucalypts and the Angophoras are characterised by the development of swellings which in many species attain a considerable size. They occur at the base of the stem either at the surface of the soil or just below it. As we shall see later, they are to be classed as tubers on both morphological and physiological grounds, and since they are woody when adult, I suggest for them the name "Lignotubers." In the great majority of forms these lignotubers merge gradually into the stem after the tree attains the young sapling stage. On the whole, their development is least in the gums, considerable in the boxes, and greatest of all in the mallees, where they persist throughout the life of the tree and attain a very large size. In the mallees these rudely globose boles, which form the mallee roots of commerce, are partly subterranean.

Attention was directed to these lignotubers by Tate,(1) who gave a brief account of the species in which he knew them to be present. Later, Jönsson(2) drew attention to them, stating that they developed under unfavourable conditions of nutrition. He considers that the nature of their growth strongly reminds one of the heteroplasmic correlations mentioned by Ernst Kuster.(3) Jönsson was able to produce these swellings or hasten their growth by cutting off the leaves, buds, or twigs.

Vueillemin(4) described these swellings as being produced by the action of a parasite, *Ustilago vrieseana,* which also produced similar swellings, which he called tumours on other Myrtaceae (Myrtus, Acmena, Tristania, Melaleuca and Callistemon). Tubeuf and Smith(5) describe them as being woody tumours, from which proceeded outgrowths resembling "witches brooms." These contained the mycelium of an Ustilago, which produced spores in the cortical tissues.

During 1909, McAlpine, at Professor Ewart's request, carefully examined specimens of these so-called diseased seedlings from the State Nurseries at Creswick, but was unable to find any trace of disease organisms. Clayton O. Smith(6) refers to these swellings as being due to infection entering through the axils of the leaves. He states that he was able to successfully inoculate seedlings of *E. tereticornis* with cultures of soil organisms.

Fletcher and Musson(7) consider that they are similar in nature to crown galls, in which the organisms are confined to the encircling tumours to which they give rise, and do not invade the rest of the stem of the seedling. They recognise three groups according to whether the Eucalypts are—(1) liable to attack, (2) resistant or refractory, (3) exempt from the attacks of the supposed parasitic soil organisms causing the tumour formation. They consider the parasites enter through the leaf axils. In addition they regard the tumours as being a drag on the normal development of the plant, and not natural growths. They published an interesting series of photographs showing the relative size of the growths and their development in different species.

Development.

Typically these lignotubers arise in the axils of the cotyledons as a pair of lateral outgrowths, which gradually increase in size until they meet, forming a swelling which encircles the stem. Pl. X., Fig. E, shows a specimen of *E. globulus,* in which fusion has just commenced. Later on, other pairs of swellings may arise in the axils of the leaves. These also increase in size, and finally fuse in pairs encircling the stem. As these further increase in size they gradually come to meet and fusion in the vertical direction takes place, resulting in a much elongated swelling, e.g., *E. amygdalina, E. elaeophora, E. sideroxylon,* etc. In cases where typically only a single pair arises, the result is a more or less rounded swelling encircling the stem, e.g., *E. globulus, E. Maideni,* etc.

By the time these swellings have attained a considerable size they have usually extended sufficiently far towards the base of the plant to encircle some of the roots. Pl. X., Fig. A, shows a specimen of *E. melliodora,* where a root has been incorporated and the encircling of a second one is commencing. In some cases secondary roots may develop from them, as shown in Pl. X., Fig. F. Under natural conditions these swellings may be considerably distorted in shape by coming into contact with hard objects, which stop their growth at the point of contact. If this occurs when the lignotubers are just commencing, it may cause the appearance of what looks like three in a whorl instead of two.

Growth under favourable conditions of nutrition results in a smooth surfaced swelling, but if subjected alternately to favourable and unfavourable conditions, they develop a very irregular surface. At certain points the bark is thinner, and after any arrest of growth by unfavourable conditions, growth is resumed most actively at these points, resulting in an irregularly lobulated surface.

There are exceptional cases in which the lignotubers occur either on the internodes after the ones in the axils of the cotyledons have appeared or one side of the stem only. In rare cases they develop on the hypocotyl below the cotyledons, as shown in

Pl. X., Fig. E. This frequently occurs in *E. corymbosa* and *E. exima,* but rarely in other species.

Considerable variation is shown in the number developed in a single species. Pl. XI., Fig. A, shows specimens of *E. numerosa,* where in one case there are as many as twelve pairs present, but where in another case in an older seedling only a single pair is present. But on the whole, the tendency is to produce a number fairly constant in the species. Thus *E. globulus, E. Maideni,* etc., normally develop a single pair of lignotubers, as seen in Pl. XI., Fig. B. while *E. sideroxylon, E. eugenioides, E. piperita, E. polyanthemos, E. coriacea,* and many others, produce many pairs. Pl. XI., Fig. A, shows a series of seedlings of *E. numerosa,* illustrating the development from a single unfused pair to a final one, consisting of a large pyriform swelling, which has resulted from the fusion of many pairs. In cases where an exceptionally large number are produced the upper ones, mainly due to the greater elongation of the internodes, may not attain a sufficiently large size to fuse with the lower ones and in such cases remain separated. This often occurs in *E. eugenioides.*

These swellings increase in size until the tree has entered on the young sapling stage, when the stem begins to thicken more rapidly than the lignotubers, and finally they become merged into the stem and disappear. In a few cases they persist throughout the life of the tree. Growing on the top of Anthony's Cutting, near Bacchus Marsh, there are three fully mature trees of *E. hemiphloia* var. *microcarpa* (Pl. X., Fig. H), and they have retained well marked swellings at the base. I have also seen several specimens of *E. sideroxylon,* and one of *E. melliodora,* which still show them in the mature tree. Although I have examined a large number I have never seen a swelling persisting in a species which inhabits the moister and better situations.

Many saplings were observed under natural conditions, and the maximum diameters of the lignotubers compared to the stem were measured together with the height of the sapling. The following are averages for species, one from a moist and three from dry localities:—

Species.	Av. diameter of the lignotubers.	Av. diameter of the stem.	Height.
E macrorrhyncha	12 cms.	5.6 cms.	210 cms.
E. elaeophora	13 cms.	6·5 cms.	300 cms.
E. sideroxylon	14 cms.	6·5 cms.	180 cms.
E. globulus var. St. Johnii	6·5 cms.	3·5 cms.	360 cms.

After this the size of the trunk increased more rapidly than that of the swelling, which remains almost the same, and gradually merges into the stem.

The species, which do not inhabit regions of uncertain climate, show no development of lignotubers. As far as I am aware, the following species show no development of them: *E. diversicolor, E. gigantea* (*E. Delegatensis*), *E. oreades, E. pilularis, E. regnans* and *E. regnans* var. *fastigata.* It is significant that all the above species inhabit regions where the rainfall is good and fairly evenly distributed throughout the year, so that there is little chance of them suffering from drought. Fletcher and Musson(7) describe *E. punctata* as being immune from these swellings, but as a matter of fact seedlings of this species show well developed lignotubers which may first appear in nursery seedlings when only twelve centimetres in height.

Species inhabiting regions which only suffer from a short period of drought towards the end of the summer attain a much greater height before they show any signs of the development of these swellings, e.g., *E. globulus, E. rostrata, E. saligna,* etc., than those in drier regions. These may attain a height of as much as 90 cms. in well lighted situations, and are from 14-30 weeks old before the lignotubers begin to appear. In the majority of cases they begin to develop when the seedlings are from 36-50 cms. high. On the other hand species inhabiting regions liable to drought develop them very early, e.g., *E. erythrocorys,* which begins to develop them as soon as it has two pairs of well developed leaves. Maiden(8) states that this species grows in the dry arid regions of Western Australia. In these situations there is usually a short wet, warm period, when growth is very active, which is followed by a prolonged dry spell. Specimens of this species in the nurseries of Messrs. G. Brunning and Son, four centimetres in height, had a pair of well-developed lignotubers each the size of a radish seed. Greenhouse specimens of *E. Priessiana* commenced to develop the swellings when six centimetres in height and eight weeks old, while *E. tetraptera* was only five centimetres in height and nine weeks old. When it was twenty-eight weeks old it possessed two pairs of swellings eleven and nine centimetres respectively in diameter.

Among the boxes, ironbarks, stringybarks and peppermints, e.g., *E. hemiphloia, E. polyanthemos, E. melliodora, E. sideroxylon, E. macrorrhyncha, E. obliqua,* and many other forms inhabiting regions of uncertain climate, the development began when the seedlings were from nine to sixteen centimetres in height and nine to twelve weeks old. The greenhouse in which these seedlings were raised is unheated and rather badly lit, consequently the lignotubers were slightly later developing, and the seedlings attained a height greater than they do under natural well lit conditions, but they serve for comparison, as all were under exactly the same conditions. In the field species, such as *E. macrorrhyncha, E. elaeophora, E. numerosa,* and many others show signs of the development of lignotubers when from four to seven centimetres in height, and when their age is not more than ten weeks at the outside. Thus on the whole, the more uncertain the climate of the locality in which a species naturally is found, the greater is the development of the lignotubers and the earlier they appear in the seedling. Thus the gums, e.g., *E. globulus, E. saligna, E. rostrata,* etc., under greenhouse conditions, develop them when from fourteen to twenty-eight weeks old, and from thirty-six to fifty centimetres or more in height, while the boxes and similar forms develop them when from nine to twelve weeks old and nine to sixteen centimetres in height, and the species from the dry arid regions of Western and Central Australia, when from eight to nine weeks old, and three to four centimetres in height. Moreover, these forms from the hot, dry interior were considerably retarded in their development by the cool summer of 1923-24, when they were under observation.

Species which develop these swellings possess a remarkable power of producing new growth either when cut down or injured by fire. A tree of *E. hemiphloia* var. *albens* cut down four inches from the ground in July, 1923, has since produced large numbers of shoots, which were removed as soon as formed (almost every week). During January of the following year, an attempt was made to remove it by burning, but four weeks later it produced fourteen new shoots from below the charred part. It was still sprouting freely in May. In contrast to this is *E. regnans,* which produces no lignotubers, and when cut down does not sprout again. In addition to their powers of producing new growth these forms transplant very readily even when not given the most careful treatment, while species like *E. regnans* only do so when handled with the greatest care.

Lack of insolation considerably retards the formation of the lignotubers, and causes a later and a smaller development. Pl. XI., Fig. D, shows two specimens of *E. elaeophora* and Fig. B. of *E. globulus* var. *St. Johnii,* one of which was grown in the full sunlight while the other was shaded by means of frosted glass. Those which were subjected to fairly intense insolation show a larger leaf area and a much greater and earlier development of the lignotubers than those which were shaded. Seedlings of *E. elaeophora* five months old under the latter conditions presented a drawn appearance, and were just commencing to develop the swellings, while in *E. globulus* var. *St. Johnii,* in a seedling eleven months old they have not commenced to fuse. In the unshaded seedling, however, fusion has taken place. This was also very striking in the field where seedlings growing in situations subjected to fairly intense insolation showed a larger and an earlier development of the swellings than those in the more shaded situations. Seedlings of *E. macrorrhyncha* and *E. elaeophora* showed the early stages of the development when from four to six centimetres in height, while those in the more shaded situations averaged twelve to twenty centimetres in height.

In handling large numbers of these seedlings one notices a very definite relationship between the leaf area and the size of the lignotubers. Seedlings bearing unhealthy or diseased foliage produced either very small lignotubers or none at all. I raised a seedling of *E. coriacea,* which later became attacked by a " witches broom " fungus. Before the fungus attacked the seedling it possessed a small pair of lignotubers, but as soon as the disease gained a hold no further development took place. The seedling developed a large amount of wood, but a scanty leaf area.

Under natural conditions the development of lignotubers in a species bearing them is not a variable but a constant feature. Seedlings raised under nursery conditions and meeting with an accident to the root system either produce no lignotubers or very small ones. Pl. XI., Fig. E, shows two seedlings of *E. coriacea* five months old—(1) had portion of the radicle removed when pricked off, and made little growth, and developed no lignotubers, while (2) is a normal seedling. Pl. XI., Fig. F, shows the same two seedlings when eleven months old. Badly drained soil produces a similar effect.

Checking the growth by removal of the growing point causes a considerable increase in the size of the lignotubers, provided that there is a fair proportion of leaf area. Keeping the seedlings in a rather small pot, and thus checking the growth produces the same result. In all cases when the most active growth of the seedling is taking place, the development of the lignotubers is at a standstill, but as soon as the rate of growth slows down, the rate of increase in the size of the lignotubers is very marked. In all cases the largest and strongest plants produce the largest lignotubers. If the lignotubers are excised they are rapidly formed again.

The application of suitable fertilisers greatly increases the size of the lignotubers. In all cases calcium superphosphate, followed by nitrates, was the most effective, while potash had but little effect. The seedlings were grown in ordinary potting soil, so that the mineral fertilisers exercised less effect than if they had been grown in sand, but even then the effect of superphosphate was very marked. In all cases the seedlings showed rapid early growth, and the lignotubers commenced to develop as soon as the rate of growth slows down, and rapidly increase in diameter. Pl. XI., Fig. C, shows three seedlings of *E. elaeophora*, grown in four-inch pots, in ordinary soil; (a) is the control, (b) was watered at intervals for six months with 1 in 10,000 potassium nitrate, and (c) with a similar solution of calcium superphosphate. The beneficial effect of the superphosphate is very striking. Similar results were obtained with *E. globulus, E. ficifolia, E. rostrata,* and *E. leucoxylon,* but failed to produce any lignotubers in *E. diversicolor.*

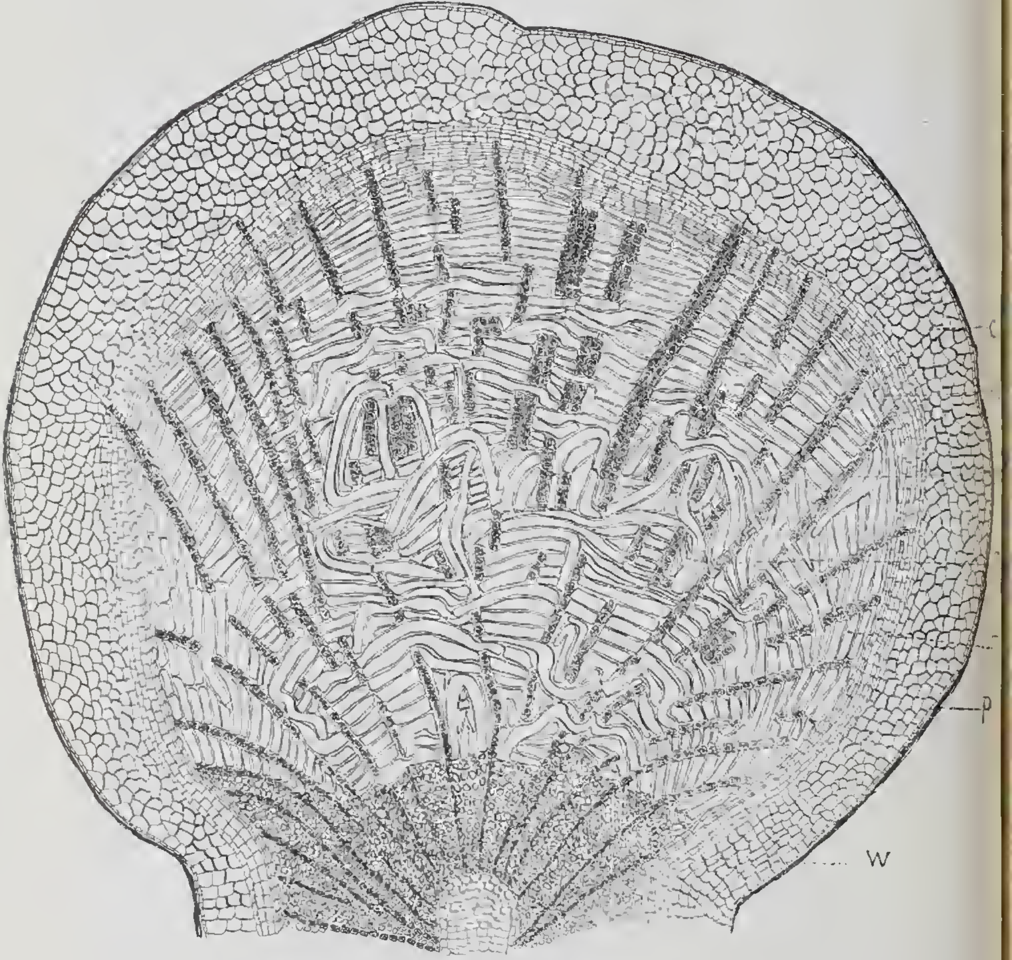
In addition to appearing on seedlings, these swellings are occasionally found on active new growth formed from a tree or a sapling which has been cut down or injured by fire. In these cases they appear towards the base of the shoot either as a single pair of lignotubers or as a number placed along the stem generally at the nodes. Pl. X., Fig. B, shows two specimens of *E. polyanthemos* five weeks and nine weeks after the removal of their shoots, which took place when they were fourteen months old. The lignotubers are developing at the nodes. Pl. X., Fig. D, shows a specimen of *E. numerosa,* the original sapling of which was attacked by Armillaria on one side in particular. A small strand of living wood remained after the sapling fell, and gave rise to the shoots bearing the lignotubers. From the dead wood a large fructification of the fungus developed, but this unfortunately was knocked off when being brought back for photographic purposes. A single specimen of *E. goniocalyx* was found where a shoot had developed directly from the root of a fallen tree. A large lignotuber developed at the base of the shoot.

The above observations seem to indicate that the lignotubers are merely embryonic storage organs developed in order to enable the seedlings to survive temporary unfavourable conditions. In support of this is the fact that the lignotubers, particularly in the species inhabiting the regions of more uncertain climate, produce large numbers of buds which, should the main stem be injured, develop and carry on the growth of the plant. Pl. X., Fig. A, shows three specimens of *E. melliodora,* in (1) the growth is carried on by the main stem, but in (2) and (3) the main stem has been removed, and the growth is carried on by shoots arising from the lignotubers. Further evidence is also afforded by the structure of the lignotubers, the nature of the food materials, and the changes which these undergo.

Structure.

The lignotubers arise in the axils of the cotyledons as proliferating outgrowths of tissue from the cambium. The greater part of the young lignotuber consists of a large number of curiously interlaced thickwalled tracheae with medullary rays occurring at intervals between them. Text-fig. I. shows a section during a very early stage of development when the twisting of the tracheae is just commencing.

These tracheae (T) develop from rows of brick shaped cambial segments which gradually elongate and fuse. As they increase in size they become much curved or twisted. Text-fig. 1 shows the twisting commencing. In all probability this results from the fact that active growth in the horizontal plane is taking place, whereas very little elongation is going on. When the lignotuber has further increased in size the twisting of the tracheae is very marked, and small rays of wood begin to appear. Text-fig. 2 shows six such rays (W). These gradually increase in size, and new ones form as the age of the lignotuber increases. Their development is usually not symmetrical, and more rays frequently appear on one side than on the other, as shown in Text-fig. 2.



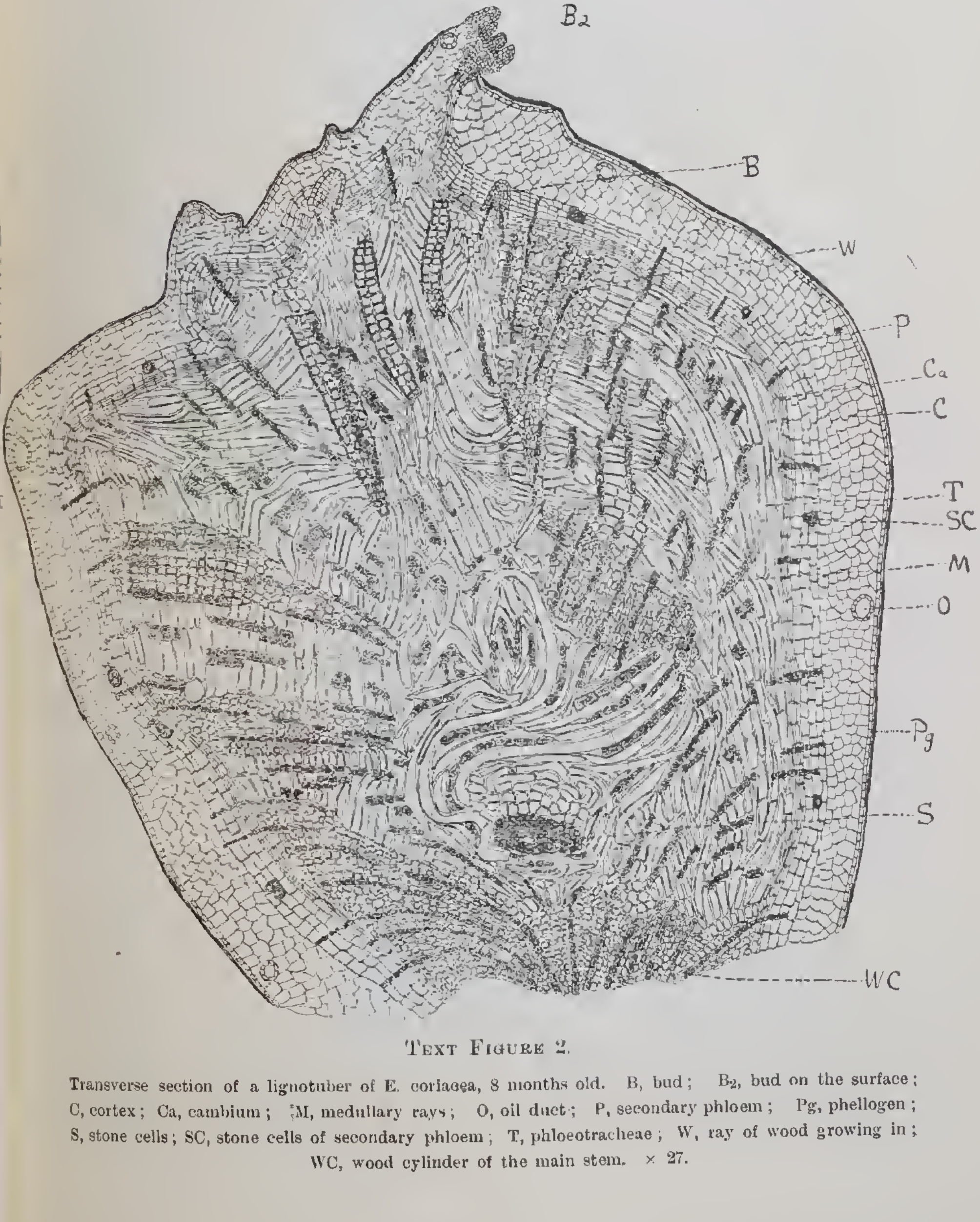
TEXT FIGURE 1.

Transverse section of a lignotuber of E. Morrisii, 12 weeks old. C, cambium; Co, cortex; M, medullary rays; P, phellogen; T, phloeotracheae; Tr, phlebotracheae enlarging and beginning to twist; W, wood of the main stem. × 31.

These rays of wood always appear at the points where growth is least active, and generally make their appearance when the lignotuber is eight to ten weeks or more old. The time of their appearance is, however, liable to considerable individual variation. In the wood tyloses are of frequent occurrence, more particularly in the wood of the main stem. At this stage also a small group of stone cells (S) appears, and occupies the position shown in the figure, which is the original centre of the swelling. In some cases other groups or more than one group, is formed.

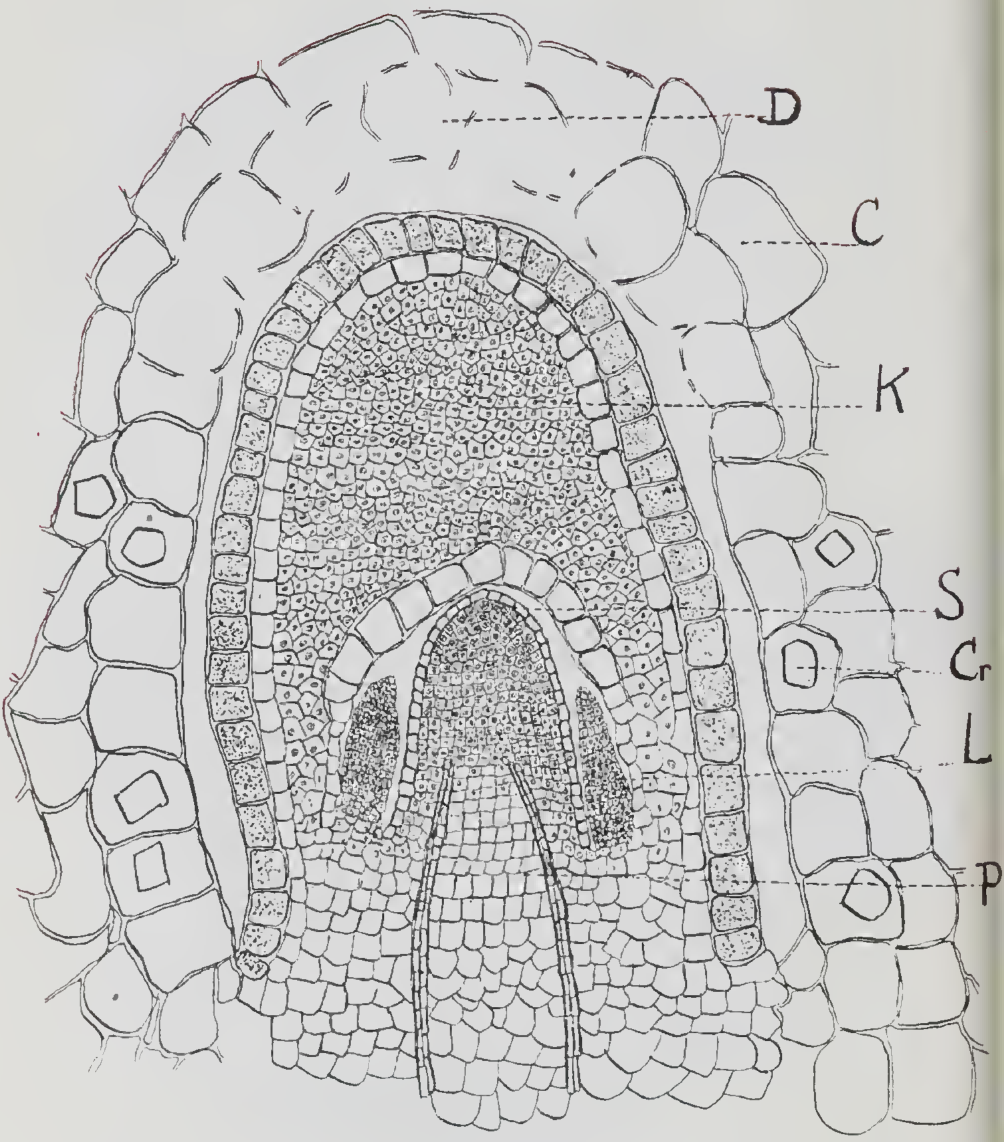
Around this group of stone cells the greatest twisting of the tracheae occurs.

Arising from the cambium are buds (B), which are peculiarly deep seated in their origin. These gradually come to lie on the surface, and give rise to new shoots as seen at (B2), which is not cut in the median plane. Very large numbers of these buds may develop, particularly if any injury should arise to the main stem when the growth of the seedling is carried on by them. Fletcher



Text Figure 2.

Transverse section of a lignotuber of E. coriacea, 8 months old. B, bud; B_2, bud on the surface; C, cortex; Ca, cambium; M, medullary rays; O, oil duct; P, secondary phloem; Pg, phellogen; S, stone cells; SC, stone cells of secondary phloem; T, phloeotracheae; W, ray of wood growing in; WC, wood cylinder of the main stem. × 27.



TEXT FIGURE 3.

Longitudinal section of a bud showing the digestive cap commencing to separate from the growing point, and the cortical cells being dissolved. C, cortex: Cr, crystals of calcium oxalate; D, disintegrating cortical cells; K, digestive cap of cells covering the growing tips; L, rudimentary leaves; P, procambial strands; S, apical meristem. × 375.

and Musson(7) describe the lignotubers as taking possession of the dormant buds and incorporating them, and that this is how these as well as the composite tumours to which they give rise come to have buds or shoots. In reality the buds are of deep-seated cambial origin, and they arise *de novo* internally, and appear on the surface later. These buds are covered by a digestive cap of cells (Text-fig. 3K) similar to that present in roots. When the bud reaches the surface of the lignotuber this digestive cap separates from the growing tip.

The cortex (C, Text-figs. 1 and 2) is narrow, and crystals of calcium oxalate are abundant in the cells. When twelve to eighteen months old phelloderm is formed (Text-fig. 4). The cells are smaller and thicker walled than the cortical cells, and also contain crystals of calcium oxalate. Oil ducts (Text-fig. 2, O) occur at intervals.

As the swelling increases still further in size, the arrangement of the parts becomes more symmetrical, and the twisting less evident, until finally it has much the appearance of a stem with broad bands of pitted tracheae (Text-fig. 4, Pt), occurring between the rays of wood (W). The tracheae from now on become shorter and wider, compared with those of the earlier stage. This structure is shown by the time the swelling is three to four centimetres in diameter, but considerable variations occur.

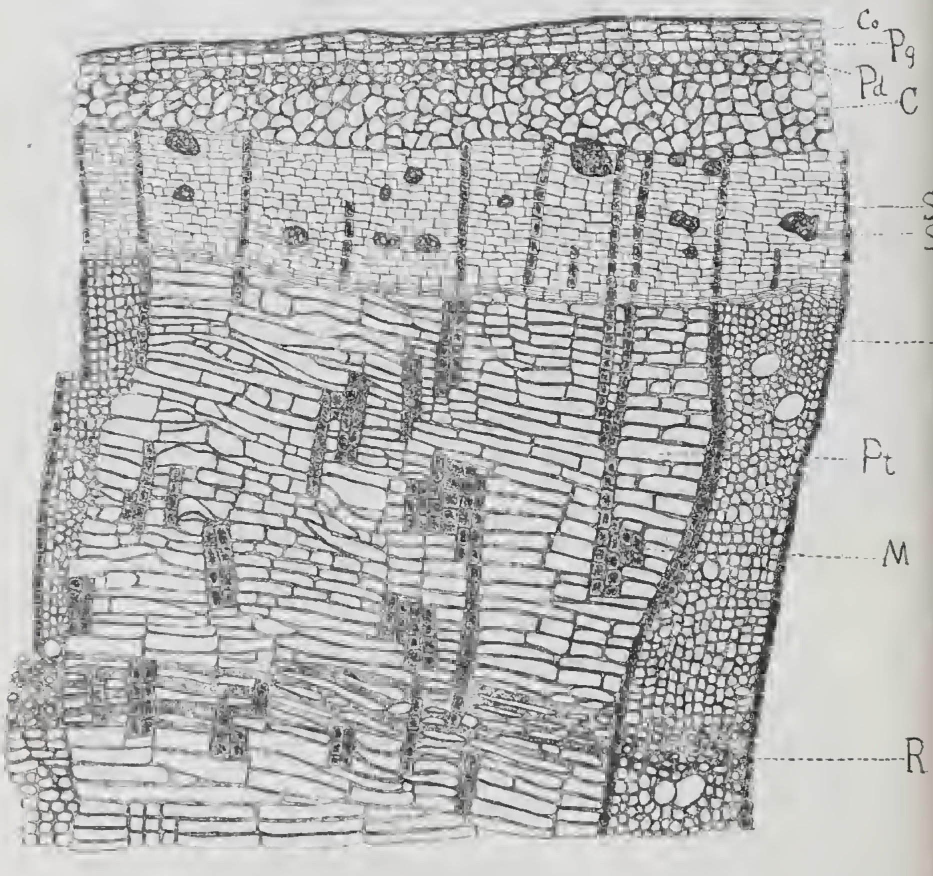
The secondary phloem is well developed with bands of medullary rays running through it. At this stage it contains stone cells (S) similar to those formed at the original centre, either in groups or as isolated cells. These also occur in many cases in the cortex. The sections show distinct bands of smaller very thick-walled elements (R), reminding one of the autumn wood in secondary growth, and which correspond to the less active periods of growth. This type of structure persists until the lignotuber attains its maximum size. After this the diameter growth of the stem overtakes that of the lignotuber, and its surface becomes continuous with that of the stem, the cambium now developing layers of wood homologous with that of the stem. Plate X., Fig. G, shows a specimen of *E. globulus* var. *St. Johnii* 6·5 cms. in diameter, where the lignotubers have commenced to merge into the stem.

The tracheae vary considerably in length, being longest during the earlier stages of growth of the lignotuber, and gradually becoming shorter and more regular in their arrangement as the swelling becomes larger. They present many features in common with the tracheids of Exocarpus, which have been called phloeotracheids by Benson. (9) For them I suggest the name of *phloeotracheae.* They are thick-walled with a particularly well developed system of bordered pits. The middle lamella is well defined, and the pits are oval in shape, with their longest axis transverse or obliquely transverse (Text-fig. 5).

The walls consist when young entirely of cellulose, but they later become lignified. The distance between the pits and the thickness of the walls varies considerably in the one section. Between the phloeotracheae the medullary rays (M) occur. When quite young their walls are unthickened, but later they become considerably thickened with pitted walls, as shown in Text-fig. 5. Occasionally ones occur with few or no pits, and much thinner walls (Mr).

The whole of the phloeotracheae and the cells of the medullary rays are packed full of food materials, the greater bulk of which is starch in the form of either simple concentric, bicompound, or tricompound grains.

The medullary rays contain small amounts of starch, and numbers of aleurone grains (A), as shown in Text-fig. 6 after special staining. The aleurone grains are circular with the

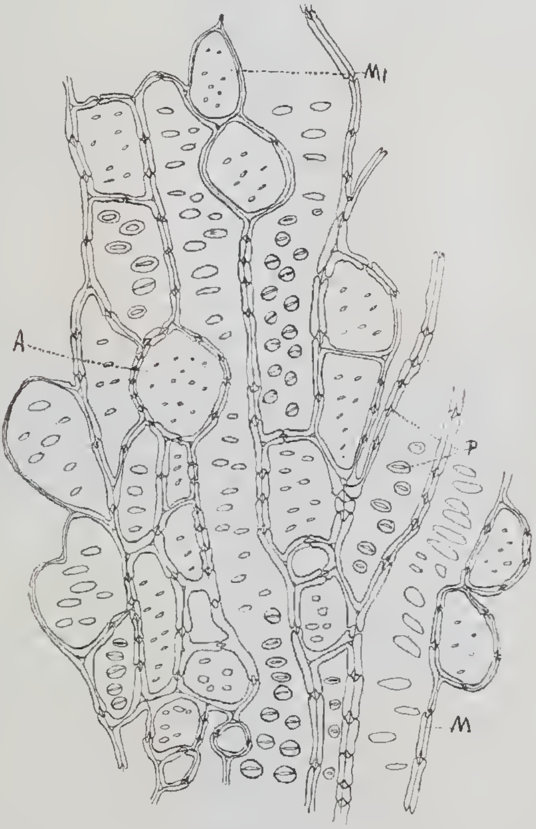


Text Figure 4.

Portion of a transverse section of a lignotuber of E. viminalis, 24 months old. C, cortex; Co, cork; M, medullary rays; Pd, phelloderm; Pg, phellogen; Pt, phloeotracheae; R, ring of thick-walled elements; S, stone cells; Sp, secondary phloem; W, ray of wood. × 51.

globoid (G) surrounded by the larger crystalloid (C). The whole is surrounded by a well defined wall (W).

Normally fats or oils (excluding essential oils) do not occur, but they may occur in species under exceptionally adverse conditions. Considerable amounts were present in a lignotuber of *E. corynocalyx* which had been inarched on to *E. robusta*. The inarching appeared to exercise an inhibitory effect on the growth of *E. corynocalyx*, and it is possible that the appearance of the oil may have been a secondary result of the influence exercised by the inarching with *E. robusta*. The normal food materials starch and aleurone were almost absent.



TEXT FIGURE 5.

Portion of transverse section of lignotuber of E. marginata, 5 months old. A, medullary ray cell with thickened pitted walls; M, middle lamella; Mr, medullary ray cell with thinner unpitted walls: P, bordered pits. × 187.

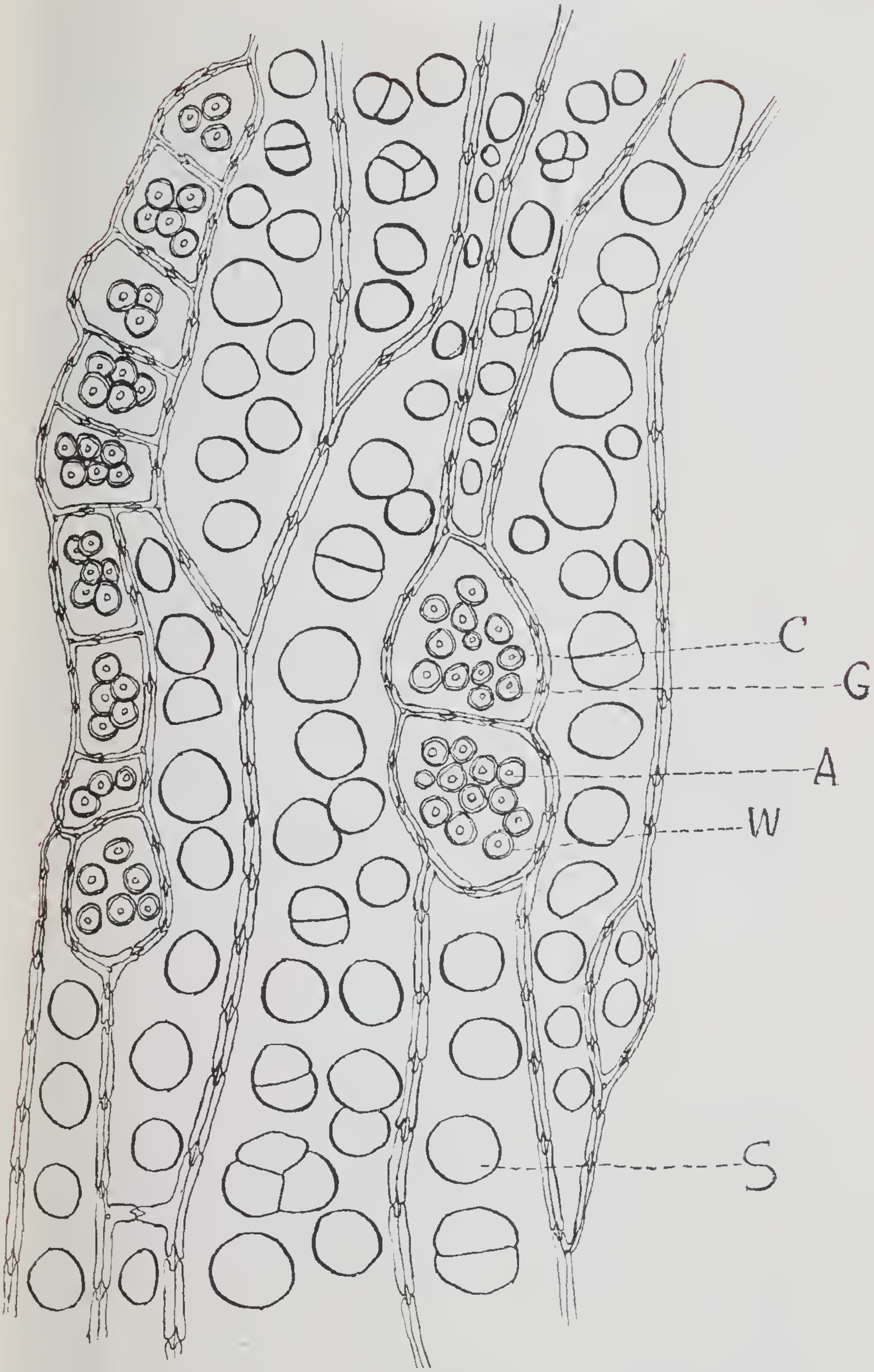
The cortex and bark are rich in a readily soluble tannin of the pyrocatechol series. Since this tannin is a glucoside in all probability it has a certain nutritive value as a reserve material.

When the seedlings are subjected to adverse or abnormal conditions which affect the plant's nutrition, the starch in the lignotubers diminishes. If the conditions are prolonged the protein food materials also diminish. These food materials are rapidly replaced on the return of normal conditions of nutrition. Drought or any condition interfering with assimilation may act in this way.

Seedlings of *E. elaeophora* 22 centimetres in height, which had been developing the lignotubers for one month, and possessed two pairs of lignotubers 0.6 cms. and 0.25 cms. in diameter, were severely injured by excessive cyaniding. In five weeks they used up all the starch in the upper (smaller) pair and half the amount present in the lower pair. At the end of the five weeks they had again resumed active growth, and in four weeks were beginning to accumulate starch again, while in eight weeks the cells were full again. The weather was cold, and this retarded the reappearance of the starch.

Seedlings of *E. globulus* 4.6 cms. in diameter grew in distilled water for fourteen weeks before completely exhausting all the supplies of food, while seedlings of *E. macrorrhyncha* and *E. elaeophora*, 22 cms. high, with a pair of swellings 0·8 cms. in diameter used all the starch and portion of the protein, and were corroding the thickened walls of the phloeotracheae after one month in distilled water. During this period the plants produced a considerable amount of new growth in excess of their rate of assimilation and this was developed at the expense of the stored food materials.

Intense cold causes a conversion of the starch to sugar, with a reversion when the temperature rises. The conversion begins by an abundant formation of soluble starch. Seedlings of *E. globulus* var. *St. Johnii*, 3.5 cms. in diameter normally contain 0.05 gms. of glucose, but after twelve days at 5° centigrade, no starch was present, and the sugar had increased to approximately 10%. The starch turns directly to glucose, and gives the characteristic osozone in abundance. Normally there is not sufficient present to do this. Seedlings of *E. macrorrhyncha* 11 cms. high, with two pairs of lignotubers, 0·76 and 0·2 cms. in diameter, after six days at 10° centigrade, showed only odd starch grains here and there, but in three days at 20° centigrade the cells were completely full again. Lignotubers of *E. globulus* var. *St. Johnii*, 3.5 cms. in diameter, after six days at 10° centigrade, had approximately half the normal amount present together, with large amounts of soluble starch, while the remaining starch grains were distinctly corroded. The normal amount was restored in three days at 20°C. Lignotubers 6 cms. in diameter required twelve days at 5° centigrade to completely transform all the starch to sugar. In four days half the normal amount was restored, and in seven days the whole. Apparently the younger lignotubers with less lignified walls can convert starch into sugar more rapidly than in the older ones. In any case this rapid con-



TEXT FIGURE 6.

Portion of a transverse section of a lignotuber of E. macrorrhyncha. A, aleurone grains; C, crystalloid; G, globoid; S, starch grain; W, wall of aleurone grain. × 375.

version of starch into sugar is of considerable interest. The presence of the sugar will lower the freezing point for the lignotuber, and will hence serve to protect it against the effects of low temperatures or frost, which might kill the more exposed or less adaptive parts of the plant.

Artificial Infection Experiments.—Several attempts were made by injecting one seedling with an extract of the lignotubers of another seedling to produce them artificially.

Text-fig. 7 shows two seedlings of *E. coriacea.* A, was inoculated with an extract from one of its own lignotubers on the internode; B, with the same extract in the axil of the cotyledon opposite an unpaired lignotuber, and in the axils of the first pair of leaves. In all cases the prick from the hypodermic needle was healed over by a callus without the least sign of a lignotuber appearing. A prick from a sterilised needle gave the same results. The following species were tried: *E. amygdalina, E. cornuta, E. numerosa, E. peltata, E. Morrisii, E. diversicolor, E. melliodora,* and *E. hemiphloia* var. *albens.*

Sterilised seeds of *E. amygdalina* and *E. elaeophora* were sown in sterilised soil. The seedlings were watered with boiled water, and grown away from external sources of infection. After the usual lapse of time lignotubers of the normal seedling character appeared. There is no evidence (1) that the lignotubers are the result of external infection, as suggested by Fletcher and Musson, (2) that they can be produced by artificial infection, as stated by Clayton O. Smith, (3) that they are produced by parasites, as stated by Vueillemin and Tubeuf and Smith. There is, however, some justification for the view that these authors have put forward. Tumours bearing a certain external resemblance to lignotubers may be produced on various eucalypts by the attacks of insects or fungi. They, however, differ in structure, are irregularly situated; persist indefinitely, and are not a constant feature of the development as are lignotubers. *E. rostrata* produces normally a pair of lignotubers, but Pl. X., Fig. C, shows two specimens with insect galls somewhat resembling lignotubers externally but differing in structure; devoid of food materials, and never becoming part of the normal tissues of the plant.

All the evidence points to the conclusion that the lignotubers are perfectly normal growths, which serve as embryonic storage organs for reserve food materials, and they represent admirable instances of the adaptive modifications of seedling eucalypts to their special conditions of life. They contain stores of food materials which enable the seedlings to tide over unfavourable periods until they are established with their root systems well into the subsoil. After this period is over there is less danger of the seedling suffering from drought, and the lignotubers merge gradually into the stem and disappear. Species inhabiting regions not liable to drought do not develop lignotubers, while their development is greatest in the species inhabiting the regions of the most uncertain climate where the necessity for them is apparent. In these situations the seedlings persist through a long hot dry summer in a few inches of soil on the top of a rocky bed. In many such cases once the seedling has developed a lignotuber it may survive two or three unfavourable periods which kill down the young seedling to the base without affecting the more resistant lignotubers which send out new shoots until its food materials are exhausted.

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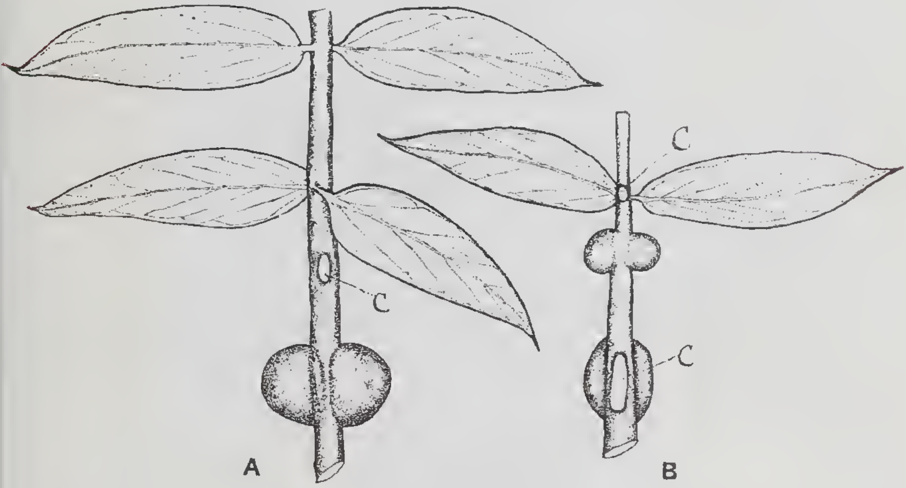

Text Figure 7.

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EXPLANATION OF PLATES.

PLATE X.

Fig. A.—*E. melliodora,* thirteen months old; 1, seedling with lobulated lignotuber with main stem carrying on the growth; 2 and 3, seedlings which have lost the main stem, the growth being carried on by secondary shoots from the lignotubers; S, main stem; M, root encircled by the lignotubers; B, root about to be encircled.

Fig. B.—*E. polyanthemos,* nineteen months old. 1, showing lignotubers resulting from the fusion of many pairs, the main stem lost, growth being carried on by secondary shoots; 2, twenty-three months old, nine weeks after the loss of the main stem; a, lignotubers developing on the secondary shoots, b and c.

Fig. C.—Two specimens of *E. rostrata,* bearing irregularly developed insect galls resembling lignotubers externally.

Fig. D.—*E. numerosa,* showing shoots from a stump bearing lignotubers; a, rotting stump, due to the attack of Armillaria; b, living strand of wood; c, lignotubers developing on the young shoots.

Fig. E.—*E. globulus* var. *St. Johnii,* twelve months old, showing lignotubers; a, which have just commenced to fuse; m, an unpaired lignotuber on the hypocotyl below the cotyledons.

Fig. F.—*E. Maidenii,* twenty-one months old, showing well developed secondary roots, r.

Fig. G.—*E. globulus* var. *St. Johnii,* showing lignotubers commencing to merge into the stems; a, secondary shoot arising from the lignotubers.

Fig. H.—*E. hemiphloia* var. *microcarpa,* showing well marked lignotubers, persisting at the base of the mature tree.

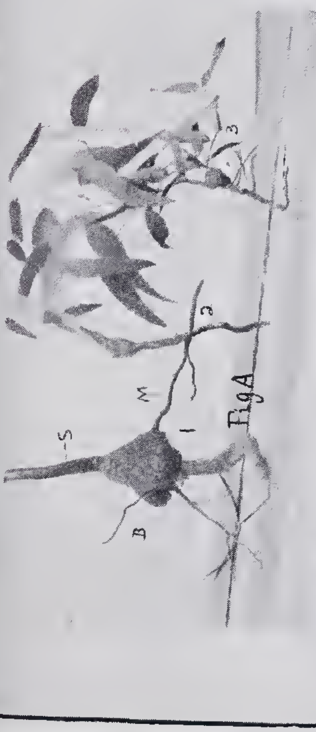

Fig A

Fig B

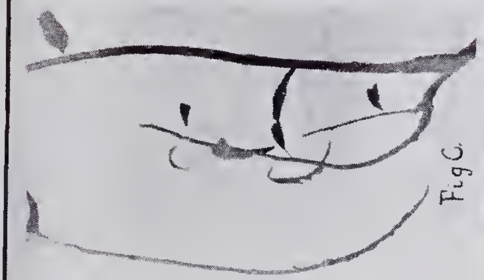

Fig C

Fig D

Fig E

Fig F

Fig G

Fig H